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RESTORATIONS OF SOME AMERICAN PERMOCARBONIFEROUS AMPHIBIANS AND REPTILES

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(WITH ILLUSTRATIONS BY THE AUTHOR)

The drawings illustrating the present paper were made in the hopes thereby of learning more concerning the animals as living organisms. Depending exclusively upon dried and petrified bones, the paleontologist is apt to forget that his fossils were once parts of living, active beings. Nearly all the restorations are based upon practically complete skeletons preserved in the museums of the University of Chicago or Yale University, technical descriptions of which have been published in various places during the past few years. Their living restorations, except that of *Eryops*, are here attempted for the first time. I will not attempt to give any technical details of their structure here; my only desire is to place before the general student of geology something of what I see, after years of study of the fauna, in some of the animals that lived in Texas and New Mexico during the closing times of the Pennsylvanian and the early times of the Permian.

The land vertebrate fauna of those times in America must have been very rich. More than forty distinct genera of amphibians and reptiles are represented in the collections of the University of Chicago, and the remains of at least a dozen more are preserved in the American Museum and at Yale University. It is the oldest fauna of reptiles known in the world, and by far the most comprehensive of the older amphibians known. The animals of the South African Karoo system are nearly all of later age, Upper Permian as distinguished from Lower Permian and Carboniferous, and they were, for the most part, more highly specialized and less primitive.

And the light these animals of the American Permocarboniferous have thrown upon the evolution of the higher vertebrates is very great, though there is very much more to learn. The primitive

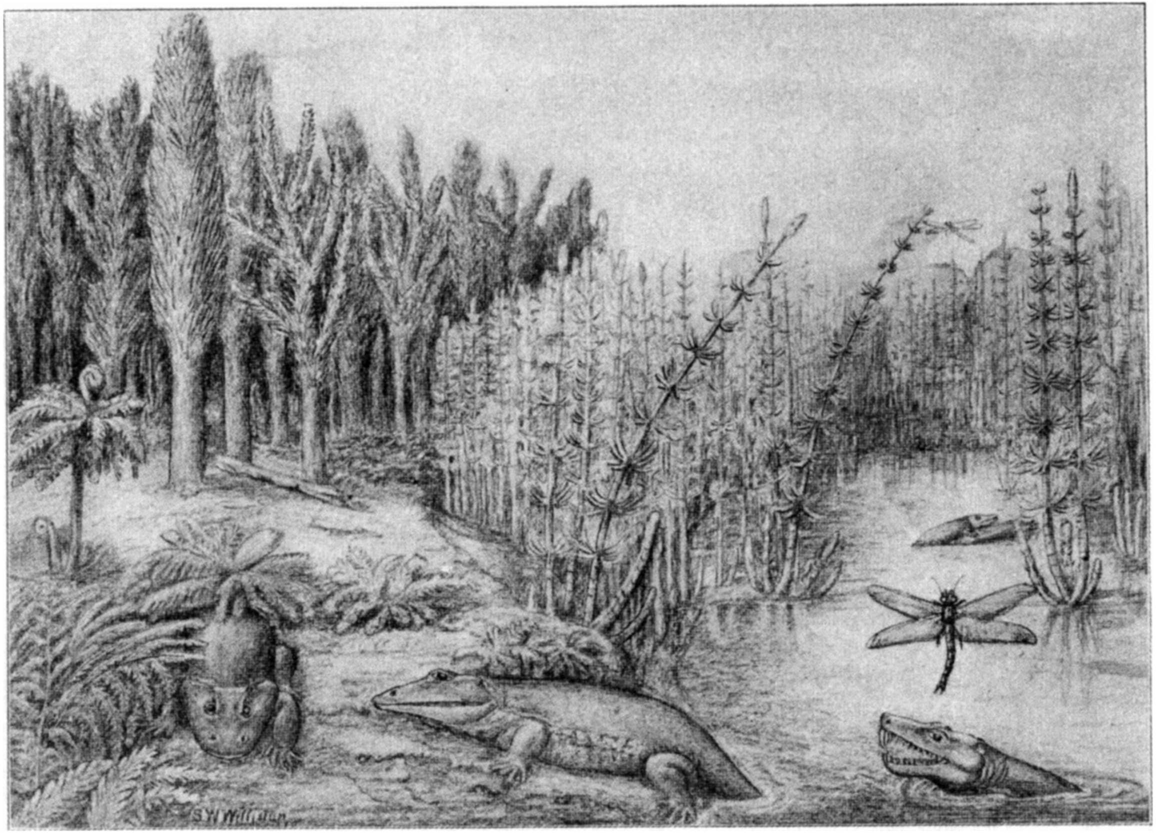

FIG. 1.—A permocarboniferous landscape, with two figures of *Eryops* upon the land, each of about seven feet in length, and *Limnoscelis*, a cotylosaur of the same length, in the water.

structure of the skull in air-breathing animals, in part at least, of the mandibles, shoulder and pelvic girdles, wrist, ankle, and digits has been determined almost exclusively from these forms.

Three very distinct groups or orders of amphibians are known from these deposits, including more than twenty known genera. The first of these groups is represented by small animals of the water which must have existed in enormous numbers. There are places in Texas where the nodules containing their remains, usually nearly complete skeletons, may be obtained literally by the wagonload. They resembled so closely in shape, and doubtless also in habits, the living *Amphiuma means* of the southern states, that a picture of that creature will almost serve for a restoration of this, which is known as *Lysorophus*. Most interesting is the fact that not only did *Lysorophus* resemble *Amphiuma* in size, shape, and habits, but it seems to be actually related to it, being the first representative known of the modern salamander type, not again known in geological history till the beginning of Cretaceous time.

A second group of very remarkable aquatic amphibians, whose relationships are still in doubt, is represented by *Diplocaulus*, a creature which reached a length of about three feet, having an extraordinary arrow-shaped head, and tiny, feebly ossified limbs of no terrestrial and little aquatic use. It, too, was a purely aquatic animal, whose remains are often found associated with those of the early sharks. A restoration of the skeleton of *Diplocaulus* will shortly be published in this *Journal* by Mr. Douthitt of the University of Chicago.

The third and most important order of all our Permocarboniferous amphibians is that known as the Temnospondyli, stegocephalians especially characterized by the divided condition of the vertebrae. They varied greatly in size, and doubtless also in habits, though none known were of upland habit. The most famous of these is *Eryops*, shown in Fig. 1 in what I have tried to represent as a characteristic landscape of the period in which they lived. It was an amphibian which reached a length of perhaps eight feet, and had a relatively large, broad, and flat head, no neck, a thickset body, and short, broad, probably webbed feet. The length of its tail is still in dispute, as may be inferred from my restorations of the creature with that part of the body hidden in the water or under the ferns. Its skin was doubtless bare, and its tail more or less flattened for use in the water, like that of a gigantic salamander, its nearest living modern relative.

There can be no doubt that the creature was amphibious, though probably not strictly aquatic in habit, like *Trimerorhachis*, remains of which are sometimes found in bone beds in great numbers. This animal, of which a restoration will be given in a future number of this *Journal*, had a more elongate and flattened head with the eyes far in front, and with almost vestigial limbs, as has *Diplocaulus*, which is often found associated with it.

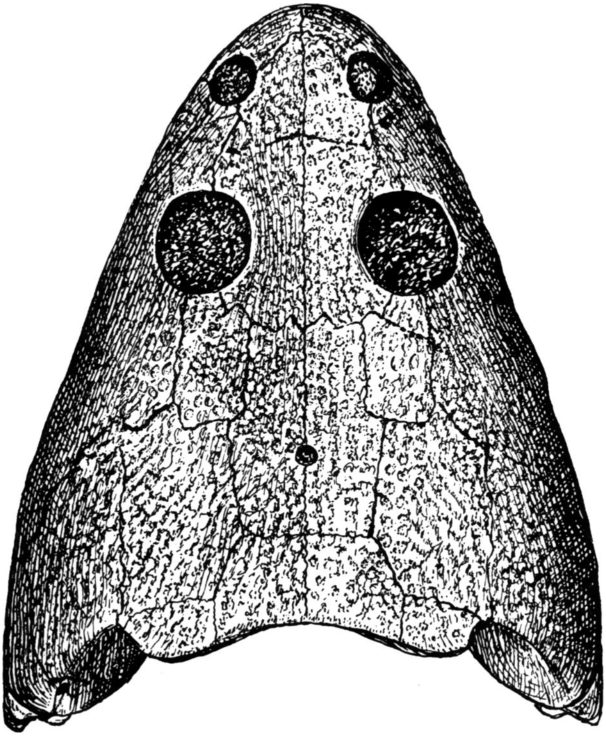

FIG. 2.—Skull of *Trimerorhachis insignis*, an aquatic amphibian about three feet in length.

Another animal of this order, which must be placed in a family all its own, the Trematopsidae, is shown in Fig. 3, as based upon the only known specimen, preserved in the University of Chicago collections, consisting of a skull in connection with body and limb bones, except the front digits, and an imperfect tail. Its restoration, therefore, is subject to minor corrections when additional specimens are found. It was more of a terrestrial animal than any other known amphibian from this fauna, though it cannot be called an upland animal, and doubtless it, too, could swim well. This creature was about two feet in length and has a relatively very large skull, fully two-thirds the length of its body to the tail. Its teeth also were more powerful than in other forms, though of the same general character. It is peculiar in showing an orifice in the skull for a facial gland, like that found in some modern amphibians.

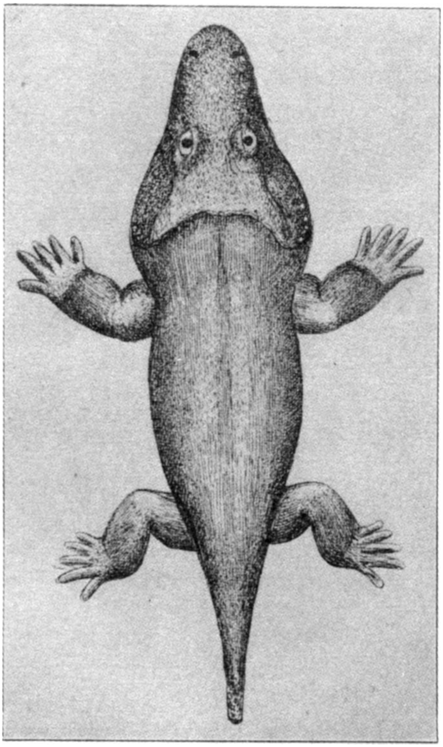

FIG. 3.—*Trematops milleri*, a stegocephalian about three feet long. From Texas

A fourth and very peculiar type of the temnospondylous amphibians is represented in the restoration of *Cacops* (Fig. 4), as based upon a marvelously complete skeleton, one of a dozen or more found associated with as many more of *Varanosaurus* and *Casea*, shown in Figs. 9 and 10. This animal, twenty inches in length, is one of a group of armored amphibians, very appositely called by Cope "batrachian armadillos," of which four or five genera are known, nearly all of the animals of approximately the same size. As suggested by Cope's name, they are all peculiarly characterized by a carapace of bony plates over the back; in some almost completely covering it, in others like *Cacops*, forming only a narrow row along the middle. In some of these has been found a peculiar bony plate in the orbits which could only have been used as a protection for the eyeball, possibly an ossification of the nictitating membrane. And one genus has the head covered with small, spiny excrescences. The ear, too, was conspicuously large, completely surrounded by bone in some, as shown. These amphibians, like most of the other small ones, must have been chiefly insectivorous, or invertebrate-feeding in habit though the presence of stout teeth on the palate suggests that any seizable living prey was acceptable as food. They were all probably lowland animals, though *Trematops* may have lived more in the forests. *Eryops*, the largest known, has a skull sometimes nearly two feet in length; other small forms associated with it have skulls no larger than one's thumb nail. Doubtless the lowlands in the vicinity of water in late Pennsylvanian and early Permian times swarmed with these creatures and with cotylosaurian reptiles of similar form and habits.

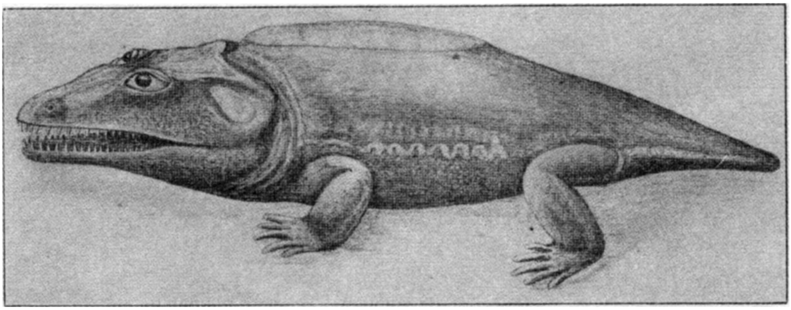

FIG. 4.—*Cacops aspidephorus*, a stegocephalian amphibian twenty inches in length. From Texas.

Varied as were the amphibians, they were not nearly so numerous or so diverse in habit and structure as were the contemporary reptiles. While it is comparatively easy to classify the amphibians, the problems which the reptiles present are vastly greater. Hitherto they have been generally classed in two main groups or orders, the Cotylosauria and Pelycosauria, but the many discoveries of recent years have broken all boundaries and opened up most complicated problems of relationships, problems which will probably not be wholly solved in many years to come. It may be twenty-five years hence before we shall have a tolerably good bird's-eye view of the complete fauna. Especially are the smaller animals, those very difficult to collect and to study, for the most part yet awaiting laborious research.

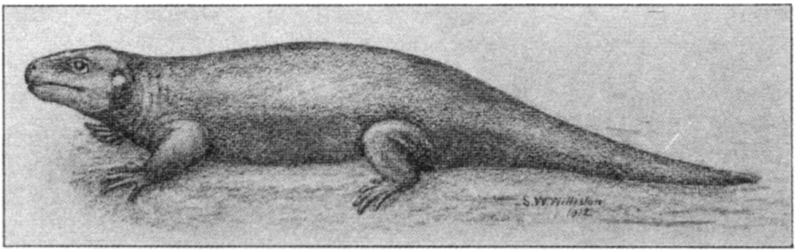

FIG. 5.—*Diasparactus xenos*, a cotylosaur reptile of about seven feet in length. From New Mexico.

But there are about one dozen of these reptiles of which we know nearly all that we may ever hope to know, forms of which complete or nearly complete skeletons have been assembled and mounted. And it is of some of these that I have attempted restorations, and will briefly discuss here.

The order Cotylosauria, whose ultimate distinctions from other reptiles consist solely of the roofed-over skull, without holes in the sides behind, and a short neck, comprises a large group of the most primitive reptiles that we know. All that are known have practically no neck, short and stout limbs, a rather thick-set body, and for the most part not very long tails. They belong to three or four groups, that have been called suborders, and six or more strongly differentiated families. The first of these is represented by *Diasparactus* (Fig. 5), so nearly related to *Diadectes* that one restoration will do for both. It is a reptile of seven or more feet in length, with short, stout legs, not very long tail, and with the head short and high, provided with crushing teeth behind and conical teeth in front. It has an enormous parietal opening in the skull, possibly suggesting a functional "pineal eye." These animals were at first thought to be burrowing in habit, because of the nature of their limbs; but burrowing would have been impossible, since by no possibility could the creatures have reached far enough forward to dig a hole for the head to enter. Nor do they show any decided aquatic characters, though doubtless they swam well.

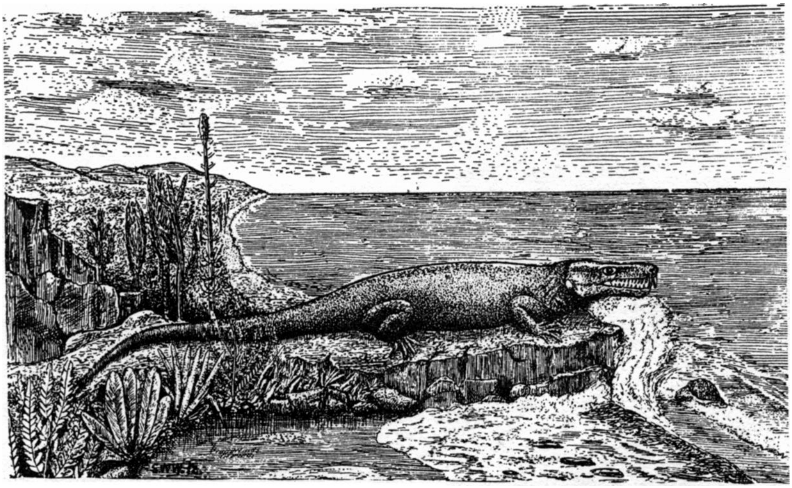

FIG. 6.—*Limnoscelis paludis*, a cotylosaur reptile, seven feet in length. From New Mexico.

Like the amphibians and most other cotylosaurs and some of the pelycosaurs, they were lowland or littoral creatures, living in and about the old lagoons and lakes.

The next type, the restoration of which is based upon a marvelously complete skeleton in the Yale Museum from New Mexico, is shown in Fig. 6, as also in part in Fig. 1. It had a much longer tail, and a more elongated and more powerful skull, beaklike in front, armed with strong, conical teeth, the foremost of which in the upper jaws were elongated and curved, as in the next group. Doubtless this was also a lowland reptile, as I have suggested in its name, *Limnoscelis paludis*, meaning marsh-footed reptile of the swamps. This reptile reached a length of seven feet, and evidently had food habits somewhat like those of the next group, though more distinctly carnivorous and rapacious.

The third group, which is composed of numerous known species, varying in length from less than one foot to more than three, is represented by *Labidosaurus* (Fig. 7). I am less certain of the precise details of this creature, since, aside from the skull, the skeletons of the Chicago collection have not been fully worked out. The restoration is based largely upon the figures of the mounted skeleton in the museum at Munich, aided by various nearly complete skeletons of smaller forms. This group of cotylosaurs, the most highly specialized of our American forms, appears to have been of more distinctly terrestrial type than the others. Its limb bones are more slender, and the claws are sharp and curved, unlike those of other groups, where they are flattened terminal nails. Especially striking is the narrowed, beaklike skull in front, and the long, curved, sharp, and rakelike teeth, which suggest their food-habit, that of prodding in the mud and sand for soft-bodied invertebrates, or possibly for detaching limpet-like creatures from the rocks. The teeth of the jaws are arranged in two or more rows, used chiefly for crushing their food, not so much for cutting or tearing.

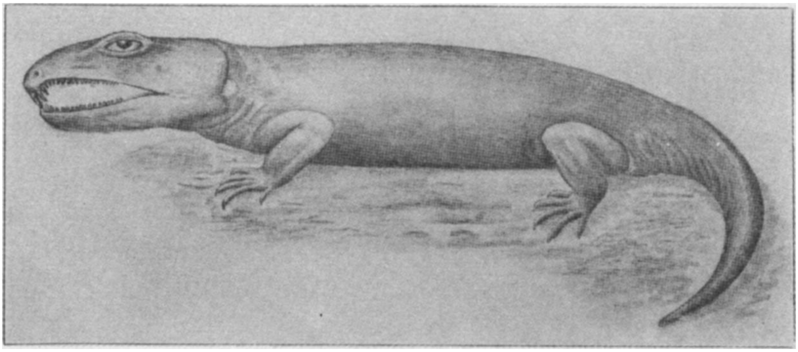

FIG. 7.—*Labidosaurus hamatus*, a cotylosaur reptile about four feet in length. From Texas.

Still another family, the most lowly organized of all cotylosaurs that are known, is represented by *Seymouria* (Fig. 8). It reached a length of not more than two feet, and had the shortest and broadest feet of all. Its skull is so nearly like that of the contemporary amphibians, especially that of some of the armadillo forms, not only in appearance, but also in actual structure, that close observation is necessary to distinguish them. The teeth are all slender and small, indicating insectivorous habits like those of the amphibians. Doubtless this too was a littoral inhabitant of more or less aquatic habit.

Still another group, one of the most peculiar of all, is unfortunately known only from the skull, of which the best specimens are in the Chicago museum, and known as *Pantylus*. In size this animal was probably no longer than *Seymouria*. It is peculiar in having a broad, flat, and firm skull with the mouth filled everywhere, on jaws and palate, with low, stumpy teeth, suitable only for crushing shellfish.

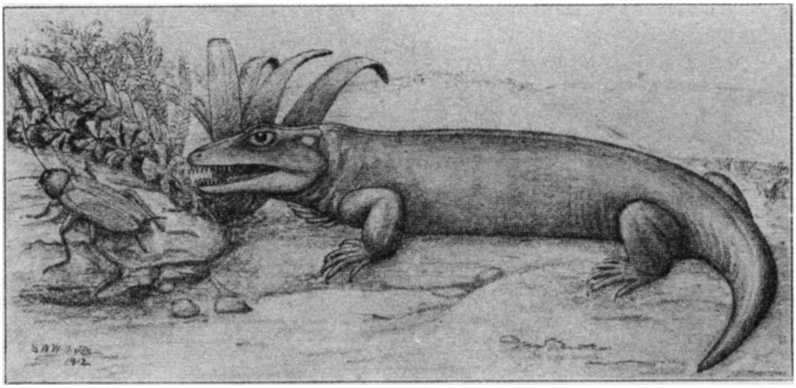

FIG. 8.—*Seymouria baylorensis*, a cotylosaur reptile about two feet in length. From Texas.

Remarkable as is the diversity of structure and habit of these primitive cotylosaurs, that of the next group, commonly called the Pelycosauria, is vastly more so. The reptiles of this group or order, which I prefer to call the Theromorpha, after Cope, are all of a distinctly higher type, especially characterized by the lightened skull, which has one or more holes in its roof behind the eyes, and by the longer neck and longer, more prehensile legs, and usually longer tails.

The best known of all these is *Dimetrodon*, various good restorations of which have been published. It was the largest of all the well-known animals of the American Permocarboniferous, especially characterized by its enormous crest, formed by the spines of its vertebrae, probably bound together by the skin. The skull was fiercely carnivorous in shape and in its teeth, and the largest species must have measured ten feet in length, though the length of the tail is not surely known. Our chief knowledge of the animal is due to Professor Case. It was the Bengal tiger of the fauna.

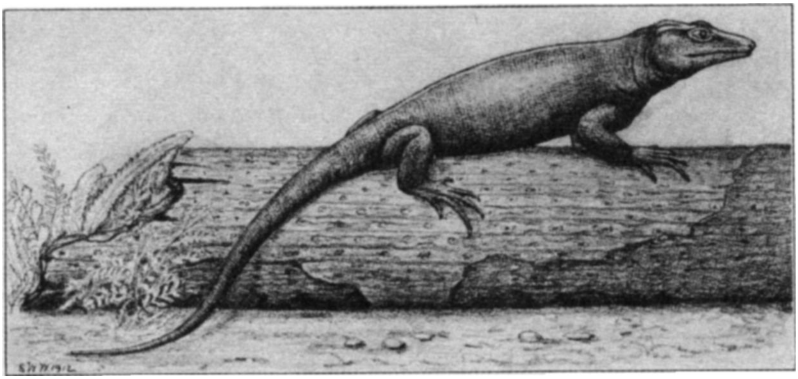

FIG. 9.—*Varanosaurus brevirostris*, a pelycosaurian reptile, forty-four inches long. From Texas.

Unfortunately the reptile whose restoration is most often seen in textbooks and popular works, as the most bizarre and the strangest of the fauna, is one whose real form and habits are very different from what they have been supposed to be. It has hitherto been called *Naosaurus* but its real name is *Edaphosaurus*, since only recently has its true skull, originally so named, been found connected with the vertebrae and with its true legs. A restoration of this strange animal will shortly be published by Professor Case.

Definitely and positively we know nearly every detail of the structure of the animal shown in Fig. 9, as *Varanosaurus*. The mounted skeleton of this reptile in the museum of the University of Chicago is one of a dozen or more found associated in a bone deposit with as many more of *Cacops* and *Casea*. This reptile attained a length of nearly four feet. It had a rather slender body, a slender tail, and rather slender legs, and was marvelously lizard-like in form, and doubtless also in habits. Its teeth are slender and pointed, and were adapted only for the capture of insects and small animals. Its claws are sharp and its toes long. Without great climbing powers, *Varanosaurus* and its allies, of which there are several genera, were fleet-running reptiles, living in the forests, hiding under logs, and feeding upon the numerous cockroaches and other insects.

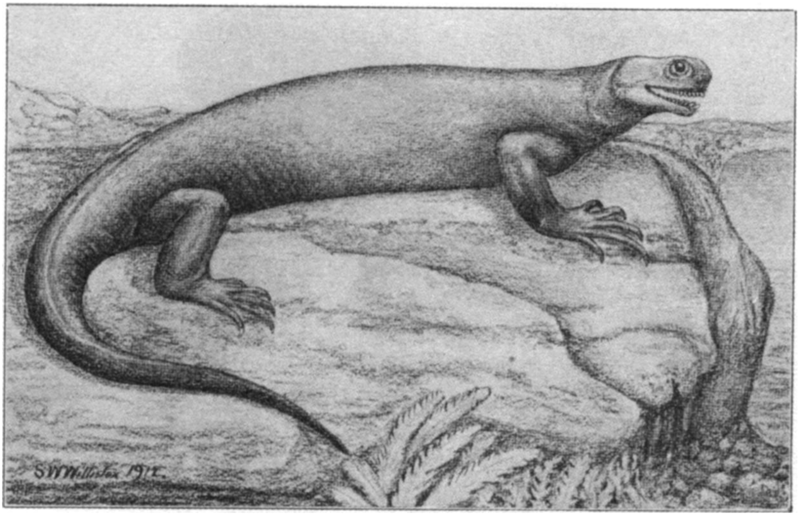

FIG. 10.—*Casea broilii*, a pelycosaurian reptile forty-three inches in length. From Texas.

Associated with *Varanosaurus* in the same deposit of bones, were a number of skeletons of *Casea*, a restoration of which is shown in Fig. 10. It, too, was nearly four feet in length, but of very different habits from those of *Varanosaurus*. Its skull was remarkably short and thickset. It, too, has a very large pineal vacuity, which curiously seems often associated with herbivorous or malacophagous habits. The teeth were relatively few in number on the jaws, but the palate was completely covered with conical teeth. Its body is extraordinarily broad and long, and of great stomach capacity; its shape is scarcely appreciable in the side view of the restoration. Its front legs were unusually powerful, and its sharp claws may have been used in burrowing. *Casea* was a relatively slow-moving, dry-land reptile.

Still more remarkable was the animal shown in Fig. 11, from New Mexico, a very perfect skeleton of which has recently been mounted in the University of Chicago museum. *Ophiacodon,* so named by the late Professor Marsh because of its slender, snake-like teeth, was fully seven feet in length, and is especially noteworthy because of its apparently enormous skull—apparently, though not really, since it is very narrow, and composed of delicate bones. The feet of *Ophiacodon* are the shortest and stoutest known among pelycosaurian reptiles, and its claws were blunt and nail-like, suggesting lowland or littoral habits, not unlike those of

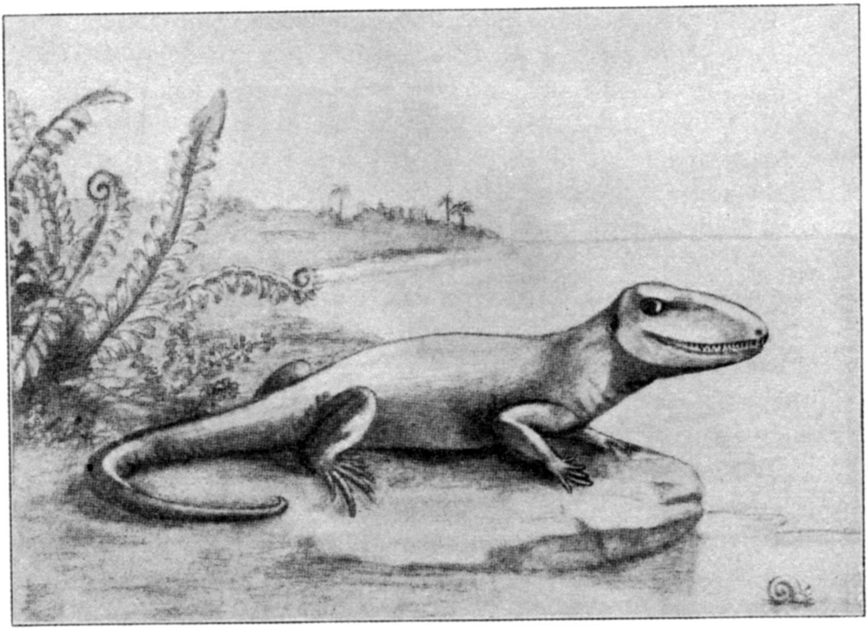

FIG. 11.—*Ophiacodon mirus*, a pelycosaur reptile about seven feet long. From New Mexico.

most cotylosaurs. Its delicate and slender teeth could have been of no use in the capture of large prey; perhaps it preyed upon the numerous small amphibians and reptiles that swarmed in such regions. And doubtless it was more or less at home in the water, though not strictly an aquatic animal. From Texas, however, a very closely allied genus—*Theropleura*—is known to have more flattened and cutting teeth, suggesting more active carnivorous habits.

Finally, the last and most divergent group of all the known paleozoic reptiles of America is represented by a little, very slender, and slender-legged reptile of about one foot and a half in length, which I have called *Araeoscelis*. A description of this animal, giving nearly every detail in its structure, is now in preparation by the writer. Suffice it to say here that *Araeoscelis* is not only wonderfully lizard-like in form, but actually lizard-like in its structure, or as nearly lizard-like as one could expect in such ancient creatures; so lizard-like indeed that I firmly believe that it was actually closely akin to the ancestors of all our lizards and snakes, without a single character that would not be expected in the most primitive lizard. *Araeoscelis* was an exceedingly fleet, climbing and running reptile of the uplands, of purely terrestrial habits.

In conclusion I may add that, whatever may be the merits of these restorations as works of art, they have been drawn with most scrupulous accuracy so far as form and proportions are concerned, the musculature derived from the study of living reptiles. And, as I have said, they are all based upon practically complete skeletons; in a few only the precise length of the tail is yet unknown, or the front toes in *Trematops* and *Cacops*.